

ALTERATIONS IN PREMATING BEHAVIOR AND PHEROMONE BIOLOGY OF GAMMA-IRRADIATED *TRICHOPLUSIA NI* (LEPIDOPTERA: NOCTUIDAE)

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Exposure of female cabbage looper pupae, *Trichoplusia ni*, to gamma irradiation at 0 to 72 hr before eclosion resulted in significantly reduced moving and calling activity of the adults. The effects were dose-related from 10 to 40 kR. Generally, irradiation in a nitrogen atmosphere slightly reduced deleterious effects, but fractionation of the radiation dose did not. Four-day-old irradiated females contained significantly more sex pheromone than untreated females, indicating that loss of pheromone is positively correlated to the amount of calling activity.

Males exposed to 20 kR or 40 kR in nitrogen were not affected in their flight response in an olfactometer to a level of synthetic pheromone ca. equal to that released by a calling female or to 0.1 × this level. The response of males exposed to 40 kR in air, however, was significantly decreased at the lower pheromone concentration.

The sterile-insect release method (SIRM) of control faces the problem of using insects of possibly inferior quality relative to their natural counterparts, caused either by colonization (Boller, 1972; and others) or additional treatments (sterilization, marking, shipping, etc.). The frequently insurmountable difficulty in separation of males from females in great numbers leads to the use of both. Laboratory competition experiments indicate that the simultaneous release of sterile females and males of some species is more advantageous than the use of only males (Szentesi *et al.*, 1973). For this reason the behavioral characteristics of treated females are almost as important as those of the males.

The sterilizing dose of gamma irradiation for male *Trichoplusia ni* (Hübner) was found to be 30 krad and inherited sterility could be induced by applying 15 and 20 krad (North & Holt, 1968). Although irradiation of adult cabbage loopers produced males that were more competitive (North & Holt, 1968) than males irradiated in pupal stage (North & Holt, 1971), the pupae are most easily handled in large quantities. Adults emerging from pupae treated with 15 krad gamma irradiation, fractionated to several lower doses, showed the same level of competitiveness as those exposed to the same single dose in the adult stage. Thus,

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as the pupal stage is more sensitive to irradiation, fractionation has been believed to produce less somatic damage in *T. ni* than a single acute dose of irradiation (Toba & Kishaba, 1973). It has also long been known that irradiation in air produces higher levels of sterility and somatic damage than in other atmospheres (especially nitrogen) (Sobels, 1963; and others), but this phenomenon has not yet been studied in detail in *T. ni*.

The precopulatory behavior of untreated female and male *T. ni* has been thoroughly reviewed by McLaughlin & Shorey (1977). Recent studies with various insect species indicate that low doses of irradiation have no immediate deleterious effects on female or male attractiveness and pheromone communication and other premating behavior are affected only at high doses (Statler, 1970; Anwar & Feron, 1971; Flint *et al.*, 1973). Stimmann *et al.* (1972) found that irradiated *T. ni* females were able to attract as many males as did normal females in the field. However, attractiveness decreased at higher radiation doses. In a similar manner, they reported that there was no difference between the attraction to a pheromone source of control males and of males treated with 30 kR gamma irradiation.

Observations on the premating activity of irradiated female cabbage loopers have not been reported. Also, data are not available on how radiation treatment alters the quantity and manner of pheromone release, the response of irradiated males to the synthetic female sex pheromone in laboratory circumstances, or the effect of a nitrogen atmosphere on both of these performances. This paper addresses these questions.

MATERIAL AND METHODS

Moving activity (MA) and calling behavior (CB) of irradiated and untreated females

Pupae originating from a laboratory strain maintained since 1972 (Leppla & Vail, 1977) were carefully selected according to eye and cuticular pigmentation to obtain adults of about the same age. The following irradiation treatments (25 pupae each) were applied 0-72 h before adult emergence: a) 0 kR (control); b) 10; c) 20; d) 30; or e) 40 kR in air; f) 40 kR in nitrogen atmosphere (5 min before, and 19 min during irradiation); g) 40 kR delivered in four 10 kR fractions in air (two fractions per day, one in the morning and the other in the afternoon); h) no irradiation treatment but exposure to nitrogen atmosphere for 24 min; and i) a second group of untreated pupae that served as the control treatment for "h". Pupae of treatments "h" and "i" were introduced into cages one day later than the others; however, statistical evaluation of results showed that "i" and "a" control groups can be considered the same.

All irradiation treatments were carried out in plastic vials, 4 × 6 cm, using a ¹³⁷Cs gamma radiation source (Gammator "M", Radiation Machinery Co.) having a dose rate of 2122 R/min. During the 4-month experimental period the average dose rate ranged from 2122 to 2110 R/min. After treatment the pupae were put into cages (25 pupae each) of 25 × 25 × 25 cm (front side made of plexiglass; all the other sides covered with screen) and provided with 10% honey water.

For observations the cages were placed on a rack in front of a white linen cloth attached to a wooden frame behind which were four rheostat-dimmed incandescent bulbs set to produce a light intensity of about 0.3 lux in the cages. By sitting in front of the rack and occasionally using a low intensity red flashlight one could easily observe different activities of moths.

Temperature and relative humidity were controlled during the observation periods at $25.3^{\circ} \pm 0.4^{\circ}$ (S.D.) and $72.9\% \pm 2.2\%$ (S.D.), respectively. Moth emergence and mortality were checked daily. A 7.5D:16.5L photoperiod, reversed from that to which the larvae were exposed, was maintained.

The numbers of females showing moving activity (MA = flying, fanning, walking, feeding) and calling behavior (CB = characteristic body posture showing an everted pheromone gland related to pheromone release) were counted alternately every 5 min during the scotophase. The hourly means of MA and CB, corrected daily for mortality and emergence, were calculated.

Surface and whole content of irradiated and untreated female pheromone glands

Female pupae handled and maintained as described above were treated as follows: a) 0 kR (control); b) 40 kR in air; c) 40 kR in nitrogen; and d) no irradiation but treatment with nitrogen for 24 min. During and after emergence the pupae and the adults were kept in 500 cm³ paper containers with screened ends and were fed honey water. A reversed photoperiod (10D:14L) was maintained.

On the 4th day after emergence, pheromone gland surface rinses in diethyl ether were made using essentially the same method described by Sower *et al.* (1973). A 30-sec rinse time per gland was employed with 17 samples (23 glands/sample) for each of the three treatments and the control. In addition, entire pheromone glands were collected in diethyl ether for the purpose of comparing gland surface pheromone concentration with total pheromone titer. Forty replicates (59 glands/sample) for each treatment and the control were prepared. Prior to sample filtration, known quantities of internal standards [(Z)-7-dodecen-1-ol and (Z,E)-9,12-tetradecadien-1-ol acetate] were added to each sample. Internal standard quantification served as an approximation of the loss of pheromone when test samples were concentrated (under nitrogen) from 4-5 ml to 0.1 ml.

The extract samples were injected into a gas chromatograph (Varian 2100) equipped with a H₂ flame ionization detector and employing a 1.8 × 2 mm id glass column (3% OV-1 on 100/120 mesh Gas Chrom Q). Column temperature was programmed for 100°-190° at 6°/min. Detector and injector temperatures were 235° and 225°, respectively. Carrier gas (N₂) flow was ca. 30 ml/min. The program employed clearly separated the cabbage looper pheromone from the two internal standards. Previously several injections of synthetic cabbage looper sex pheromone [(Z)-7-dodecen-1-ol acetate] of known concentration (1 µg/µl) were made for direct quantification of the sample peaks. The quantity of pheromone/sample was calculated on the basis of two injections/sample. Final estimates of the pheromone content of individual females were made following corrections for loss during concentration and for the volume of each injection.

Response of irradiated and untreated males to synthetic pheromone

Male pupae were treated as described earlier except that an additional treatment with 20 kR gamma radiation was also used. The olfactometer and pheromone injection system is described by Mayer (1973) and the bioassay technique was that published by McLaughlin *et al.* (1974). The olfactometer bioassay technique briefly was as follows: males were preconditioned in the tunnels before bioassays and tested during a reversed scotophase at ca. 0.3 lux. Each plexiglass olfactometer tunnel (30 × 30 × 350 cm, with an air flow of 3.7×10^4 cm³/sec) was divided into three compartments isolated from each other by wire screens. The insects were placed into the rear compartment, and the pheromone dispenser was introduced 277 cm upwind. After removal of the screens the males were allowed to perform an upwind flight toward the pheromone source for 30 sec; then the wire screens were replaced and the number of insects was counted for each compartment. Bioassays were conducted at $22.5^\circ \pm 0.6^\circ$ (S.D.) and $66.0\% \pm 0.5\%$ (S.D.) RH. The 2- to 5-day-old males (20 for each group in a single bioassay) were exposed to either 1.4 or 14 ng/min (ca. equivalent to one female) of the synthetic female sex pheromone [(Z)-7-dodecen-1-ol acetate, >99% purity]. The response of males to each concentration and treatment was tested twelve times.

RESULTS

MA and CB of irradiated and untreated females

There was no indication of an adverse effect upon female survival following irradiation of pupae during a 6-day period of observation (Table I).

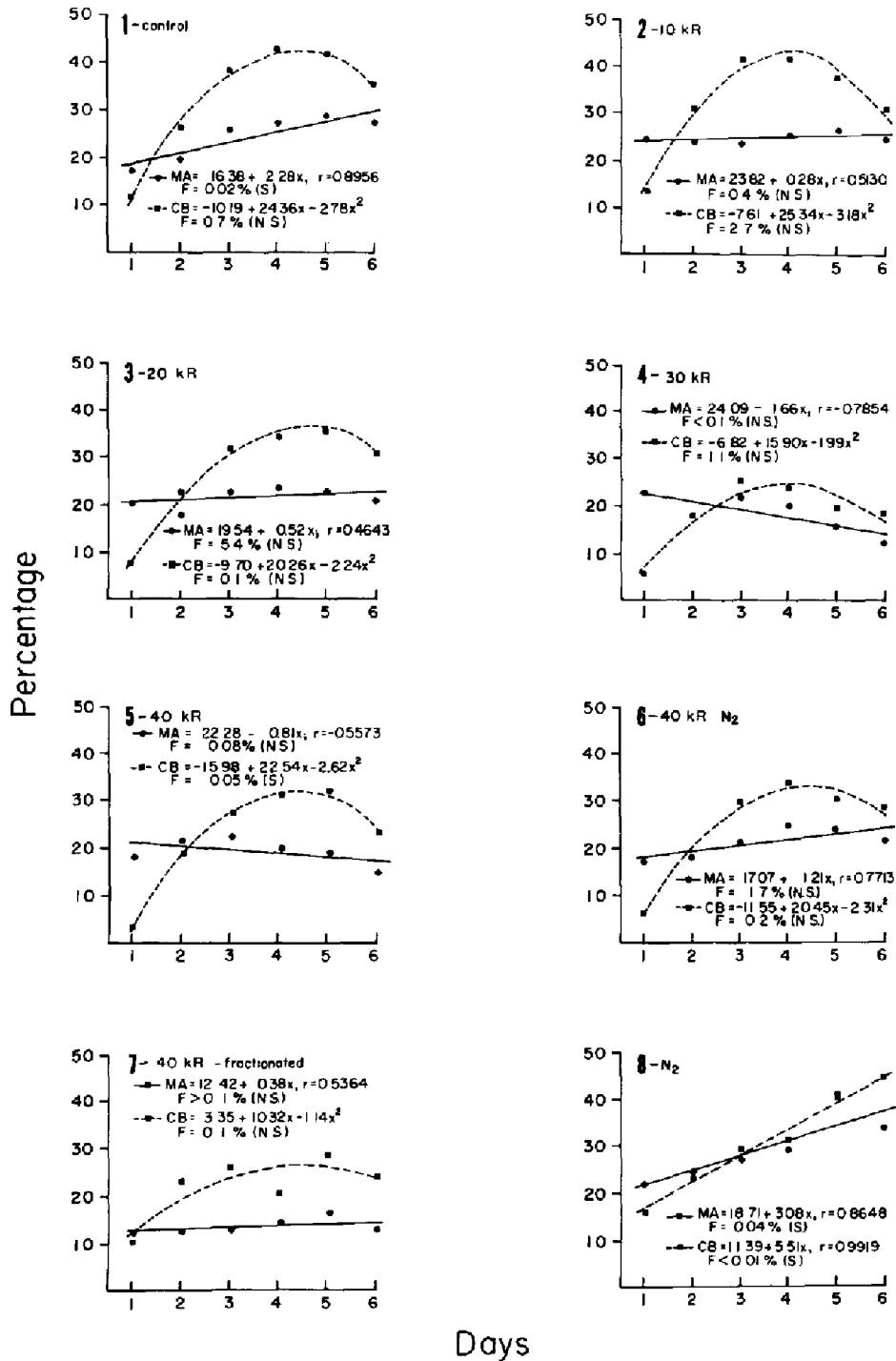
Irradiation treatment significantly affected MA and CB at all doses except 10 kR (Table II). A 10 kR exposure showed a slight stimulating effect, though daily MA and CB were not significantly different from those of the control (Figs 1, 2). The MA of the control and nitrogen-treated females (Figs 1, 8) showed a continuous significant increase as moths aged. However, the rate of increase

TABLE I

Number of living T. ni females during the 6-day observation of moving activity and calling behavior

Treatment (kR)	Numbers * of females alive on day					
	1	2	3	4	5	6
0 (control)	16.5	21.5	22.0	19.5	19.0	18.5
0 + nitrogen exposure	17.5	20.0	19.5	18.0	17.0	17.0
10	13.5	19.5	24.0	24.0	23.5	23.0
20	13.0	20.5	24.0	23.5	22.5	22.0
30	13.5	20.5	23.5	24.0	24.0	23.5
40	9.0	17.5	23.0	23.0	23.0	22.5
40 + nitrogen exposure	16.0	20.5	23.0	23.0	22.5	22.0
40 in four fractions	16.5	23.0	23.0	22.5	21.5	20.5

* Calculated by adding the total number of emerged adults from the previous day to the mean of daily emergence of the next day and subtracting mean daily death.



Figs 1—8. Percentage of daily moving activity (MA) and calling behavior (CB) of *T. ni* females treated as indicated.

TABLE II

Comparison of effects of various treatments on average daily moving activity (MA) and calling behavior (CB) of T. ni females

Treatment (kR)	Percent MA *	Percent CB **
0 (control)	25.6 a	33.0 a
0 + nitrogen exposure	29.6 b	29.9 b
10	24.9 a	32.8 a
20	21.6 c	27.3 c
30	17.6 d	18.6 d
40	19.5 cd	23.2 ef
40 + nitrogen exposure	22.0 c	25.0 e
40 in four fractions	13.5 e	21.6 f

Each mean is an average of 42 * and 46 ** values and 288 observations, respectively. Duncan's new multiple range test. Means followed by the same letter are not significantly different at the 1% level.

declined as the result of the 10 and 20 kR treatments (Figs 2, 3). The 30 and 40 kR irradiation resulted in sharply decreasing MA (Figs 4, 5). Here the slopes of regressions became negative, and both treatments produced very sedentary females. Although 40 kR irradiation in nitrogen atmosphere tended to increase MA and CB performance (Table II, and Fig. 6), they did not differ from a single 40 kR radiation exposure in air. Dose fractionation (Table II, and Fig. 7) unambiguously produced as deleterious an effect on both MA and CB as did the 40 kR single dose treatment. Exposure to only nitrogen produced the highest MA values; the CB was similar to a lower (ca. 15 kR) irradiation treatment (Table II, and Fig. 8).

Generally, there were no significant correlations of daily MA and CB with moth age. However, MA values for the untreated (control) (Fig. 1), CB values for 40 kR radiation-treated (Fig. 5), and MA and CB values for females unirradiated but exposed to nitrogen (Fig. 8) did show significant correlations with female age.

TABLE III

Correlation between moving activity (MA) and calling behavior (CB) of treated and untreated T. ni females

Treatment (kR)	Correlation coefficients	Relationship *
0 (control)	0.7216	S.
0 + nitrogen exposure	0.6422	S.
10	0.6482	S.
20	0.4439	N.S.
30	0.6060	S.
40	0.7327	S.
40 + nitrogen exposure	0.6870	S.
40 in four fractions	0.2444	N.S.

* S = significant; N.S. = not significant.

TABLE IV

Mean (\pm S.D.) surface and whole gland pheromone content of untreated and irradiated 4-day-old T. ni females

Treatment (kR)	No. of samples (1) + (2)	Pheromone content (ng/female) \pm S.D.	
		On the surface (1)	Of the whole gland (2)
0 (control)	4 + 9	25 \pm 8 A	266 \pm 65 a
0 + nitrogen exposure	3 + 11	29 \pm 13 A	275 \pm 84 a
40 + nitrogen exposure	3 + 10	51 \pm 21 A	554 \pm 154 b
40	3 + 10	51 \pm 16 A	667 \pm 155 b

Means in the same column followed by the same capital or small letters are not significantly different at the 1% confidence level. (Duncan's new multiple range test for unequal sample size).

Significant correlations were also found between the daily MA and CB of all except the 20 kR and the fractionated 40 kR treatments (Table III). With these treatments, daily MA remained nearly constant (cf. Figs 3 and 7).

Surface and whole gland content of pheromone glands of irradiated and untreated females

Gland surface pheromone content. The quantity of pheromone obtained from the gland surfaces of females, irradiated in the presence or absence of nitrogen, was greater than that obtained from untreated females (Table IV); however, this tendency was not statistically significant and individual samples were highly variable. During elaboration of samples for GC analysis an average of 21.4% \pm 14.9% (S.D.) loss of pheromone was detected.

Whole gland pheromone content. There was a highly significant difference between normal and irradiated female pheromone gland contents (Table IV). The

Table V

Response of treated T. ni males to different concentrations of synthetic female sex pheromone in olfactometer

Treatment (kR)	% (\pm S.E.) responding males to pheromone concentration	
	1.4 ng/min	14 ng/min
0 * (control)	60 \pm 8 aA	71 \pm 5 aA
0 + nitrogen exposure	68 \pm 5 aA	76 \pm 3 aA
20	61 \pm 5 aA	68 \pm 4 aA
40 + nitrogen exposure	55 \pm 7 aA	69 \pm 4 aA
40	35 \pm 7 bB	62 \pm 5 aA

Means marked with the same capital letters are not significantly different between pheromone concentrations. Those followed with the same small letters are not significantly different between irradiation or atmospheric treatments at the 1% confidence level (Duncan's new multiple range test).

* Acetone-treated dispensers alone gave a response of 16% \pm 1.9% (mean \pm S.E. of 46 tests conducted concurrently by M. S. Mayer of this laboratory).

greater the irradiation dose the higher the quantity of pheromone that was found in the glands. Irradiated 4-day-old female glands contained an average of 2.5 times more pheromone than the glands of untreated females. A minimum of 150-200 ng/female difference in pheromone content was statistically significant. There was a slight positive (less pheromone) but not significant effect when irradiation was done in N_2 .

The preparation of whole gland pheromone extracts resulted in an average of $34.6\% \pm 15.5\%$ (S.D.) loss of pheromone.

Response of irradiated and untreated males to synthetic pheromone

Table V shows the responses of treated males to synthetic pheromone in olfactometer tests. Radiation treatments tended to reduce male response to the pheromone. However, only a very high, single dose treatment of 40 kR gave a result significantly different from other treatments when the males were tested with the lower pheromone concentration. Irradiation in nitrogen atmosphere seemed to provide a substantial protection compared with the same or other doses without nitrogen exposure. Differences and tendencies among various irradiation effects were more pronounced in tests conducted at the lower pheromone concentration. A tenfold difference in pheromone concentration increased the response ratio highly.

DISCUSSION AND CONCLUSIONS

We have found that treatments with increasing gamma irradiation doses and with the exception of 10 kR as a stimulating exposure, caused gradually increasing deleterious effects on the behavior of *T. ni* females and males. The treated females tended to move less and although CB was not entirely inhibited by irradiation, a 5%-11% decrease did occur in comparison with the untreated female CB activity. Considering that in laboratory circumstances about one half (Sower *et al.*, 1971) or less (Table II, control females CB) of the mature *T. ni* females show premating behavior and pheromone release on any given night, the 5%-11% decrease in the number of calling irradiated females may substantially affect the impact these females would have on a native population. Even a single nitrogen exposure had a significant adverse effect upon CB (Table II). A similar study with *Plodia interpunctella* adults (Brady & Smithwick, 1968) also showed a marked effect on calling. This experiment does not allow us to draw a conclusion about the mechanism of irradiation effect on these behavioral patterns.

Although MA and CB correlate, this correlation does not seem very strong and showed variations in the course of different treatments (Table III). The data suggest that MA and CB are affected at the same time but not always to the same extent by the same treatment.

We believe that our findings are in agreement with the data of Stimmann *et al.* (1972) in regard to *T. ni* and those of others (Barlett *et al.*, 1968; Statler, 1970) with other species. They proved that irradiation did not affect female (or male)

attractiveness though in none of the studies MA and CB were directly observed. Stimmann *et al.* (1972) found that irradiated *T. ni* females became increasingly less attractive to males as the dose increased. The irradiation treatments probably do not affect the pheromone emission rate of a female in a direct way but do influence CB, which is a necessary behavioral step prior to pheromone emission. The overall quantity of pheromone, emitted by a released sterile female population should be smaller and also, as a consequence, the number of males responding.

Data obtained on pheromone content of gland surface rinses and of whole gland extracts contradict earlier findings of Shorey & Gaston (1965) and Sower *et al.* (1972). They found that the amount of pheromone in virgin females quickly reached a maximum (ca. 1000 ng) within 1-2 days after emergence. This level remained about the same during calling (an expenditure of 7 ng/min/female) and after one copulation (Shorey & Gaston, 1965; Shorey *et al.*, 1968). Histological examinations seemed to prove the same because no further change was detected in the gland structure during 1-7 days after emergence (Jefferson *et al.*, 1966). An early rapid accumulation and an even faster synthesis of the pheromone during its release seemed to be the likely explanation. This was further supported by the observation that no storage organ for newly synthesized pheromone was found. However, in our study untreated cabbage looper females at 4 days of age contained only ca. 300 ng/female, considerably less than 1000 ng. On the other hand, the irradiated females, which exhibited significantly less CB, contained a significantly greater quantity of pheromone (often approaching 1000 ng/♀ in individual samples). This finding suggests that female *T. ni* do expend pheromone that is not replaced by synthesis.

The amounts of pheromone obtained from whole glands throughout the 2 months of our study were not highly variable (see Sower *et al.*, 1972), and the relationships between treatments remained constant. Therefore, the differences found between treatments (Table IV) are presented with a good deal of confidence. An explanation for the difference found between the pheromone content of irradiated and untreated females could lie in the fact that radiation decreases calling activity in females; therefore, they expend less pheromone than untreated females.

The results obtained from olfactometer tests using untreated and irradiated male cabbage loopers, exposed to two concentrations of synthetic pheromone, showed that the males were not affected seriously by irradiation doses sufficient to give complete sterility. Only 40 kR significantly depressed the male response, and a tenfold increase in pheromone concentration revealed that the response level established by the irradiation treatment, is dose-dependent according to the stimulus intensity (concentration) applied. These results are also comparable to those obtained in the field by Stimmann *et al.* (1972). We also found that up to 30 kR there were no differences in the males' response, and even the significant decrease by 40 kR treatment may only be of theoretical interest because this dose is too high for practical application.

The exposure of 40 kR-treated pupae in a nitrogen atmosphere resulted in as good performance of males as those of the control or from all other treatments. Thus, nitrogen may provide a method for reducing the deleterious impact of irradiation on male pupae.

The general changes which can be characterized as sedentary behavior of irradiated female *T. ni* manifested themselves in behavioral traits such as a decreased CB. For instance, the pheromone content difference between treated and untreated females appears to be a result of their behavioral differences, not biochemical differences.

The recently applied 20 krad dose, which gives partial sterility in *T. ni*, and the subsequent release of both sexes in a field experiment (Lingren¹, pers. comm.) indicated that the treated insects were competitive and that the SIRM can effectively suppress wild cabbage looper populations. However, the broad spectrum of physiological changes, for example, in vision (Holt, 1975), in flight (Sharp & Chambers, 1977), in locomotory activity (Bailey, 1975), in mating competitiveness, etc., evoked in various species by irradiation, each have a behavioral manifestation. These changes may decrease the probability for success in a SIRM program.

In conclusion, we can state that the dosages currently used in most SIRM projects, probably affect the pheromone communication behavior of the irradiated insect species.

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Mention of a commercial or proprietary product in this paper does not constitute an endorsement of that product by the authors or their supporting agencies.

ZUSAMMENFASSUNG

VERÄNDERUNGEN IM VORKOPULATIONSVERHALTEN UND IN DER PHEROMONBIOLOGIE BEI GAMMABESTRAHLTEN *TRICHOPLUSIA NI* (LEPIDOPTERA: NOCTUIDAE)

Puppen von *Trichoplusia ni* wurden 0-72 Stunden vor dem Schlüpfen der Falter einer Gamma-bestrahlung ausgesetzt. Die Bestrahlung betrug 10-40 kR und erfolgte entweder in Luft (ununterbrochen oder fraktioniert) oder in einer Stickstoffatmosphäre. Die Effekte der verschiedenen Behandlungen auf das Rufverhalten der Weibchen (CB), die Bewegungsaktivität (MA) und den Pheromontiter wurden beurteilt. Die Reaktion bestrahlter Männchen auf das synthetische Sexualpheromon (Z-7-Dodecen-1-ol-azetat) wurde gemessen bei einer Konzentration, wie sie von einem Weibchen erzeugt wird, und bei einem Zehntel dieser Menge.

¹ Lingren, P. D. Research Developments Related to the Planning and Conducting of a Pilot Test for Cabbage Looper Population Suppression Through Releases of Partially Sterile Adults Irradiated as Pupae. Presented at the Cabbage Looper Conference, National Meeting of the Entomological Society of America, November 28, 1973, Dallas, Texas.

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Die Bestrahlung reduzierte bei sitzenden Weibchen gesichert CB und MA (Tabelle II). Die Reduktion dieser Aktivitäten war im allgemeinen dosisabhängig. Die Fraktionierung der Bestrahlung und die Bestrahlung in Stickstoffatmosphäre konnten diese Effekte nicht gesichert vermindern.

Bestrahlte Weibchen riefen gesichert weniger als nicht bestrahlte Tiere und gaben weniger Pheromon ab. Als Folge davon enthielten ihre Pheromondrüsen im Alter von 4 Tagen gesichert mehr Pheromon als Drüsen unbehandelter Weibchen (Tabelle IV).

In Olfaktometertests reagierten Männchen, die mit bis zu 40 kR bestrahlt worden waren, ungefähr gleich wie unbestrahlte Männchen, wenn sie einer Verdampfungsrate von einem Weibchenäquivalent des Pheromons ausgesetzt wurden (Tabelle V). Männchen, die mit 40 kR in Stickstoffatmosphäre behandelt worden waren, reagierten auf eine niedrigere Pheromonkonzentration gleich gut wie Männchen, die mit 20 kR in Luft behandelt worden waren. Sie waren gesichert reaktionsfähiger als solche, die mit 40 kR in Luft bestrahlt worden waren.

Die mögliche Bedeutung dieser Effekte für das Autozidverfahren wird diskutiert.

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